

# OBSERVATIONS ON TETRAMEROUS DISC FLORETS IN THE COMPOSITAE

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During the course of a systematic study of the genus *Lipochaeta* DC. (Compositae, Heliantheae) from the Hawaiian Islands, it was noticed that certain species are characterized by having four-lobed disc corollas and four anthers (referred to as tetramerous disc florets), while other taxa have typically five-lobed disc corollas and five anthers (pentamerous disc florets). These observations have led to an interest in the occurrence of the tetramerous condition within the Compositae and its taxonomic significance. The present paper attempts to improve our understanding of this phenomenon by: (1) summarizing the known distribution of the tetramerous condition of disc corollas within the family; (2) commenting on the possible ontogenetic and genetic factors influencing corolla lobe number; (3) offering suggestions for possible adaptive significance of the change to the tetramerous state; and (4) discussing the taxonomic significance of the tetramerous condition within different groups of the family.

## DISTRIBUTION WITHIN THE FAMILY

The occurrence of tetramerous disc florets within the Compositae is relatively wide-spread, having been reported for more than 80 genera in nine of the 13 tribes (Table 1). The important points of the information presented in Table 1 are that the tetramerous condition occurs within many separate evolutionary lines, and that frequently both tetramerous and pentamerous florets are found in the same genus. Although reported for a few genera, this phenomenon is not common in the discoid or ligulate tribes. There is no apparent correlation between the occurrence of the tetramerous state and geographical distribution, as this condition is found almost equally in taxa of both the tropical and the temperate areas of the world.

## ONTOGENY AND GENETICS

Floret development has been studied in several Compositae genera: e.g., *Aster* and *Solidago* (Martin, 1892); *Chrysanthemum*



Table 1. Genera of the Compositae possessing tetramerous corollas<sup>a</sup>

Genus	Number of Corolla Lobes <sup>a</sup>	Number of Species <sup>b</sup>
<b>Vernonieae</b>		
<i>Rolandra</i> Rottb.	4	1
<i>Spiracantha</i> Kunth	4, 5	1
<i>Struchium</i> P. Br.	3, 4	1
<b>Eupatorieae</b>		
<i>Kanimia</i> Gardn.	4	14
<b>Astereae</b>		
<i>Bellis</i> L.	4, 5	7
<i>Bellium</i> L.	4, 5	3
<i>Calotis</i> R. Br.	4 <sup>c</sup>	20
<i>Dicrocephala</i> DC.	4, 5	13
<i>Egletes</i> Cass.	4, 5	12
<i>Grangea</i> Adans.	4, 5	6
<i>Grangeopsis</i> H. Humb.	4 <sup>c</sup>	1
<i>Keysseria</i> Lauterbach	4	15
<i>Laestadia</i> Kunth	4, 5	6
<i>Microtrichia</i> DC.	4, 5	1
<i>Myriactis</i> Less.	4 <sup>c</sup>	12
<i>Psiadiella</i> H. Humb.	4 <sup>c</sup>	1
<i>Remya</i> Hillebr.	4 <sup>c</sup>	2
<i>Rhynchospermum</i> Reinw.	4, 5	1
<i>Thespis</i> DC.	4	1
<b>Inuleae</b>		
<i>Angianthus</i> Wendl.	4, 5	30
<i>Athroisma</i> DC.	4	8
<i>Epaltes</i> Cass.	3-5	15
<i>Evax</i> Gaertn.	4, 5	15-20
<i>Filago</i> L.	4, 5	50
<i>Gnephosis</i> Cass.	4, 5	12
<i>Micropsis</i> DC.	4, 5	5
<i>Millotia</i> Cass.	4, 5	4
<i>Myriocephalus</i> Benth.	3, 4	10
<i>Nanothamnus</i> T. Thoms.	4	1
<i>Quinetia</i> Cass.	4, 5	1
<i>Rutidosis</i> DC.	4, 5	7
<i>Sphaeranthus</i> L.	4, 5	40
<i>Stuartina</i> Sond.	4, 5	2
<i>Stylocline</i> Nutt.	4 <sup>d</sup>	6
<i>Symphyllocarpus</i> Maxim.	4	1
<i>Thespidium</i> F. Muell.	4	1
<i>Toxanthes</i> Turcz.	4, 5	2



Table 1 (Continued)

Genus	Number of Corolla Lobes <sup>a</sup>	Number of Species <sup>b</sup>
<b>Heliantheae</b>		
<i>Abasoloa</i> La Lave	4	2
<i>Adenocaulon</i> Hook.	4, 5	5
<i>Coreopsis</i> L.	4, 5 <sup>c</sup>	120
<i>Eclipta</i> L.	4, 5	4
<i>Glossocardia</i> Cass.	4	2
<i>Lantanopsis</i> Wright	4	2
<i>Lindheimera</i> A. Gray & Englm.	4, 5	1
<i>Lipochaeta</i> DC.	4, 5 <sup>f</sup>	28
<i>Moonia</i> Arn.	4 <sup>g</sup>	1
<i>Oparanthus</i> Sherff	4 <sup>h</sup>	2
<i>Petrobium</i> R. Br.	4 <sup>i</sup>	1
<i>Riencourtia</i> Cass.	4, 5	8
<i>Sclerocarpus</i> Jacq.	3-5	15
<i>Spilanthes</i> Jacq.	4, 5	60
<i>Synedrella</i> Gaertn.	4	50
<i>Thelesperma</i> Less.	4, 5	12
<i>Trichospira</i> Kunth.	4	1
<b>Helenieae</b>		
<i>Amauria</i> Benth.	4 <sup>j</sup>	3
<i>Closia</i> Remy	4	10
<i>Correllia</i> Powell	4 <sup>j</sup>	1
<i>Eutetras</i> A. Gray	4 <sup>j</sup>	2
<i>Helenium</i> L.	4, 5	40
<i>Laphamia</i> A. Gray	4	20
<i>Lasthenia</i> Cass.	4, 5 <sup>k</sup>	16
<i>Pericome</i> A. Gray	4	4
<i>Perityle</i> Benth.	4	25
<i>Rigiopappus</i> A. Gray	3, 4	1
<i>Thymopsis</i> Benth.	4	2
<b>Anthemideae</b>		
<i>Abrotanella</i> Cass.	4	14
<i>Centipeda</i> Lour.	4	4
<i>Ceratogyne</i> Turcz.	3, 4	1
<i>Cotula</i> L.	4	80
<i>Elachanthus</i> F. Muell.	3, 4	1
<i>Isoëtopsis</i> Turcz.	4	1
<i>Lidbeckia</i> Bergius	4	2
<i>Matricaria</i> L.	4, 5	4
<i>Nanothea</i> DC.	4	1
<i>Peyrousea</i> DC.	4, 5	2



Table 1 (Continued)

Genus	Number of Corolla Lobes <sup>a</sup>	Number of Species <sup>b</sup>
<b>Anthemideae (Cont.)</b>		
<i>Plagiocheilus</i> Arn.	4, 5	7
<i>Schistostephium</i> Less.	4	12
<i>Soliva</i> Ruiz & Pav.	4	9
<i>Thaminophyllum</i> Harv.	4	2
<b>Senecioneae</b>		
<i>Eriothrix</i> Cass.	4, 5	2

<sup>a</sup>Bentham & Hooker, 1873. The list of genera was compiled mainly from this source, although especially large genera (*Vernonia*, 1000 spp., *Erigeron*, 200 spp., *Helichrysum*, 500 spp., and *Centaurea*, 600 spp.) were excluded because of the apparently infrequent occurrence of tetramerous corollas in these taxa. Representative specimens of most of the genera were examined by the author and additional data were added from the articles cited below.

<sup>b</sup>Harborne *et al.*, in press; this is the total number of species comprising the genus.

<sup>c</sup>Grau, in press.

<sup>d</sup>Correll & Johnston, 1970.

<sup>e</sup>Smith, 1972.

<sup>f</sup>Gardner, unpubl.

<sup>g</sup>Stuessy, 1975.

<sup>h</sup>Stuessy, in press a.

<sup>i</sup>Stuessy, in press b.

<sup>j</sup>Powell & Turner, 1974.

<sup>k</sup>Ornduff, 1966.

(Popham, 1963); *Lactuca* (Jones, 1927); *Tagetes* and *Tragopogon* (Sattler, 1973). Generally, the first stage of corolla development can be seen as five protuberances around the margin of a floret primordium. The tube is formed by intercalary growth of cells below these protuberances. As the corolla elongates, stamen primordia develop alternate to the lobes, with further elongation resulting from intercalary growth below the stamen primordia (Esau, 1965). Florets are initiated acropetally until all available space on the receptacle is occupied (Popham, 1963). Presumably, this generalized developmental sequence also could be observed in tetramerous disc florets, but I know of no study which provides such documentation.

In many Compositae one can observe an occasional tetramerous disc floret in a predominantly pentamerous capitulum. This possibly can be explained in terms of the crowding of floral



primordia. Apparently the number of florets initiated is a function of the receptacle size and whenever the space from one primordium to an adjacent one is sufficiently small, four lobes develop rather than five (R. A. Popham, personal comm.). This explanation also could be applied to the situation seen in heads with predominantly tetramerous disc corollas. In these taxa it is possible that there has been an increase in the number or size of the floral primordia, without a proportional increase in apex size, resulting in crowding of florets and the initiation of four lobes rather than five. The tetramerous species of *Lipochaeta* produce from 70% to 100% four-lobed disc corollas. In those taxa which do not produce all tetramerous florets, 70% of the pentamerous ones are found in the outer two whorls of the disc. At the time of floret initiation there could be slightly more space available toward the outside of the head. If there is more space, one might expect more pentamerous disc florets to develop there. The need for developmental studies to help understand how and why tetramerous disc florets develop seems apparent.

As for the genetic factors regulating corolla lobe number, it is possible that in at least some taxa the morphological change in number of corolla lobes and stamens is a mechanical consequence of polyploidy. Within *Lipochaeta*, 10 of the included species have tetramerous disc florets while the remaining 18 are pentamerous. Two different ploidy levels are found within the genus;  $n = 15$  and  $n = 26$ . Preparations of cells from the higher numbered group show 26 bivalents with from one to four much smaller dark-staining bodies. These bodies are interpreted as centric fragments, indicating an aneuploid reduction from the tetraploid number of  $n = 30$ . To date, 15 of the 28 species have been determined chromosomally (Gardner, unpubl.). Of these, eight are diploid, while seven are tetraploid. The diploids uniformly have pentamerous disc florets and the tetraploids are consistently tetramerous. In *Lipochaeta*, there is an obvious relationship between polyploid level and number of corolla parts. Experimental studies designed to elucidate the connection between these two features are needed.

#### POSSIBLE ADAPTIVE SIGNIFICANCE

Very little has been written about tetramerous disc florets in the Compositae, and therefore, there is next to no information on



the adaptive significance of this morphological change. Some speculations, however, might be useful at this time.

First, one might speculate that a change from the pentamerous to the tetramerous condition is related to a change in breeding system from chasmogamy to autogamy. Assuming no other morphological alterations, a floret with four anthers would produce less pollen than one with five anthers. If less pollen is required to insure fertilization within a selfing head as compared to one that is outbreeding, such a change would result in a more energetically efficient system. This has been shown to be the case in *Lasthenia* of the Helenieae (Ornduff, 1966). Along with numerous other morphological changes, the self-pollinating tetramerous *Lasthenias* produce less pollen per floret than their outbreeding pentamerous relatives. With respect to *Lipochaeta*, reduced pollen production does not seem to be correlated with tetramerous disc florets. Comparisons of pollen grain number estimates show that the tetramerous *Lipochaetas* produce as many or more grains per floret than the pentamerous species. Little is known, however, about the breeding systems within the genus.

Second, it is possible that a change from the pentamerous to the tetramerous state can be explained in terms of selective pressures for increased reproductive potential. In *Lipochaeta*, the tetramerous taxa, on the average, produce ten more florets per head than the pentamerous species. As discussed in a previous section, tetramerous disc florets might result when the distance from one floral primordium to an adjacent one is sufficiently small, this reduced distance from one floret to the next resulting in more florets, i.e., more seeds, produced per head. This idea would fit into Stebbins' (1974) "line of least resistance" theory. That selective pressures for increased reproductive potential have existed (and still do exist) in *Lipochaeta* can be inferred from a consideration of the relative success of the tetramerous vs. pentamerous taxa. With the exception of two species (out of 18), each of the five-lobed *Lipochaetas* has a very restricted distribution, e.g.: *L. exigua*, two localities in the Hoary Head Range of Kauai; *L. waimeaensis*, a single gulley on the west side of Waimea Canyon of Kauai; *L. kamolensis*, Kamole Gulch on southern East Maui; etc. The tetramerous species on the other hand are very common, many of them becoming weedy in certain areas, e.g.: *L. rockii*, known from several localities on central Molokai



through the west end of that island; *L. heterophylla*, commonly encountered on three different islands, Molokai, Maui, and Lanai; *L. lobata*, very common around Kaena Point and from Diamond Head to Waimanolo Beach on Oahu. Assuming the chances for seedling survival are the same, the success of the latter species could be due in part to greater seed production.

#### TAXONOMIC SIGNIFICANCE

The usefulness of a consistent morphological feature (e.g., the number of floret parts) as a taxonomic character is dependent upon its proven efficacy in a particular instance. In the case of the tetramerous condition, its taxonomic utility, in combination with other useful characters, is known from the subtribal to the infraspecific level. The subtribe Peritylinae of the Helenieae is characterized by having genera that are primarily tetramerous (Powell & Turner, 1974). In *Coreopsis* (Smith, 1972, 1975) and *Lipochaeta* (Gardner, unpubl.) tetramerous disc florets are significant at the sectional level. In the previously mentioned work of Ornduff (1966) with *Lasthenia*, the number of corolla lobes is a useful character at the specific and infraspecific levels.

The occurrence of four-merous corollas is not only significant for descriptive taxonomy but is also valuable for constructing phylogenetic schemes. As evidenced by its rarity (present in only about 80 or 1250 genera), the tetramerous character state is probably derived within the entire family. In addition, detailed studies on individual genera such as *Coreopsis* (Smith, 1975), *Lasthenia* (Ornduff, 1966), and *Lipochaeta* (Gardner, unpubl.), indicate a derived status for the tetramerous condition within these taxa. It is realized that evolutionary reversals might have occurred from the tetramerous back to the pentamerous state, as is known to happen in other apparently directional features (Eyde, 1971; Stebbins, 1975), but it is hoped that this evaluation will alert other workers to the potential of this feature in determining evolutionary trends within the groups they study.

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